

THE CORPUS LUTEUM IN CERTAIN OVIPAROUS AND VIVIPAROUS REPTILES.

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(Plates ix-xiv.)

[Read 31st October, 1934.]

Introduction.

The need for a comparative study of the corpus luteum in oviparous and viviparous reptiles becomes apparent when the facts concerned in the present transitional state of the reptilian reproductive cycle from oviparity to viviparity are considered. Among certain reptiles (lizards and snakes) there are oviparous species which lay their eggs after a short retention of only a few weeks within the oviducts; ovo-viviparous species which hold eggs within the oviducts for a longer and variable period, perhaps, as in *Anguis fragilis*, for almost as long as the life of the embryo in the egg in the nest; and, finally, truly viviparous species from which the young are born without egg-membranes, after a gestation period of approximately three months. The viviparous species vary further among themselves, some having no apparent reduction in the yolk-content of the ovum at the time of ovulation and a simple allanto-placenta, presumably for respiration (Weekes, 1927), and others with an obvious reduction in yolk-content and a comparatively complex small allanto-placenta for the nutrition of the embryo (Harrison and Weekes, 1925).* Here is excellent material for an investigation of the rôle played by the corpus luteum in these reptiles during the variable periods of retention, and it is with such an investigation that this paper is concerned.

In 1892 Strahl described "Die Rückbildung reifer Eierstockseier im Ovarium von *Lacerta agilis*", in 1893 Mingazzini published a paper on "Corpi lutei veri et falsi dei Rettili", and in 1903 Lucien wrote a "Note préliminaire sur les premières Phases de la Formation des Corps Jaunes chez certains Reptiles". More recently Hett (1924) described in detail the development and structure of the corpus luteum in *Lacerta agilis*, but as far as the author can ascertain no attempt has been made to make a systematic or comparative study of the corpus luteum of oviparous and viviparous reptiles.

Lizards were examined in Europe and Australia. In the Australian oviparous lizard *Amphibolurus muricatus*, and the Australian viviparous lizard *Lygosoma (Hinulia) quoyi*, a complete study was made of the development and structure of the corpus luteum from the stage immediately following ovulation to the time

* Much of the work referred to in these introductory remarks is embodied in a paper by the author which will probably be published shortly in an English journal.

of the complete disappearance of the corpus luteum from the ovary. Corpora lutea in six other species of viviparous lizards were examined at various stages during pregnancy and after the birth of the young. These were (a) the Australian *Egernia whitei*, *E. cunninghami* and *Lygosoma (Hemiergis) quadridigitatum*, three lizards with no apparent reduction in the yolk-content of the ovum at the time of ovulation and with a simple allanto-placenta presumably for respiration (Weekes, 1930); (b) the Australian lizards *Lygosoma (Liolepisma) weekesae* and *L. (L.) entrecasteauxi*, the latter with an obvious reduction in yolk-content and both with a specialized allanto-placenta presumably for the nutrition of the embryo (Weekes, 1929), and (c) the European viviparous lizard *Lacerta vivipara* which has a simple allanto-placenta. There were no stages available early enough for an investigation of the yolk-content of the ova of *L. (L.) weekesae* or *L. vivipara* at the time of ovulation.

The material was collected in Australia regularly twice a week from the beginning of September until the end of February during 1932-1933 and 1933-1934, and in Europe, in the Auvergnès, the Pyrenees and the French Alps, during July, August and September of 1931.

For advice on the use of fixatives I am indebted to Miss R. Deanesly, University of London (University College), who advised Ciaccio's fluid for general cytological detail. Bouin's and Zenker's fluids were also used, but Ciaccio's fixative gave the best results (Deanesly, 1930b). The ovaries were sectioned at 7μ or 8μ . Iron haematoxylin was used after all fixatives and as counterstains, eosin and Van Gieson were used.

The corpus luteum in the oviparous lizard Amphibolurus muricatus.

A. muricatus is common around Sydney, New South Wales, measures from six to ten inches in length and lays from three to seven eggs at each breeding season. No viviparous Amphibolurid has so far been recorded. In the summer of 1932-1933, when investigations were first begun, the facts observed indicated two breeding seasons during that summer. The lizards first examined, on the 26th September, were non-pregnant and the ova in the ovaries were comparatively small. During the ensuing four weeks the ova were obviously developing toward maturation and ovulation and the first pregnant female was collected on the 28th October. Between the 28th October and the end of November all the females, as well as having eggs within their oviducts, had several enlarged ova within the ovaries. During the first week in December the eggs were laid, and of the sixteen females examined in the second week of December, fifteen were non-pregnant, with ova almost ready for ovulation and a second breeding season. Between the middle of December and the end of January all the females collected were pregnant. The ova in the ovaries of these lizards were quite small and there were no preparations for a further breeding season. Apparently all the eggs were laid by the end of January, for during February none of the lizards collected were pregnant.

During the summer of 1933-34 there was no such regularity of breeding habit. Pregnant females were first collected on the 20th September, five weeks earlier than the first pregnancy of 1932, and from the 20th September until the 30th December both pregnant and non-pregnant lizards could be collected at any time, the pregnant lizards carrying eggs at different stages of development. After the 30th December no pregnant lizards were collected.

During the earlier months, September, October and November, the pregnant lizards examined also carried enlarged ova within the ovaries, but the lizards examined in December had no enlarged ova and apparently were not preparing for a further breeding season in spite of the favourable climatic conditions of January. Therefore it does seem probable that each lizard has no more than two breeding seasons each summer.

From the facts observed then, *A. muricatus* has more than one breeding season each summer, probably two, prepares for the second breeding season while still pregnant, and the several breeding seasons may or may not occur regularly among lizards of the same locality.

The structure of the ovum and its follicle is essentially the same as that described by Hett (1924) for *L. agilis*, in which the follicle cells in early stages of development are of two kinds, both small and considerably enlarged (Figure 3 on Plate xiii is an illustration of a young follicle of *L. (L.) weekesae*). Immediately prior to ovulation the largest ova measure approximately 10 mm. in diameter and are surrounded by a thin covering of sheath tissue of two or three layers of greatly stretched fibrous connective tissue cells. At this stage there is no distinction between theca externa and interna.

The structure of the follicle immediately after ovulation.—Many lizards were collected having eggs within the oviducts without shell or even shell membrane, and with no visible signs of the beginnings of segmentation. Only one lizard was opened while the ova were actually ovulating. In this lizard there were three ova in one oviduct and three were closely packed together in the body cavity at the entrance of the other oviduct in which there were already two ova. All the large ova had been expelled from the ovaries.

With the collapse of the follicle, after the expulsion of the ovum, the relaxed sheath tissue is much thicker than in the stretched condition and there is now a definite distinction between theca externa and interna. The theca externa is more fibrous than the theca interna and contains the large blood vessels. The theca interna consists of layers of irregularly arranged cells of indefinite cell limits with oval, lightly staining nuclei of various sizes. The theca interna cells are associated with connective tissue fibres, capillaries and spindle-shaped cells of the fibroblastic type. These theca interna cells are probably a less differentiated form of the fibroblasts. As a result of the collapse of the follicle the follicular epithelium is much folded (Plate ix, fig. 5), and torn fibrous connective tissue, capillaries and loose corpuscles may be caught up between the folds. The epithelial cells are cuboid with characteristic spherical, lightly-staining nuclei and relatively deeply staining cytoplasm. At this stage these cells all show the same reaction to staining reagents. The burst follicle measures approximately 2.5 mm. \times 1.5 mm.

The corpus luteum in early stages of development.—Copulation among the lizards was not observed, so that it cannot be used as a gauge in estimating the age of the corpus luteum in its various stages of development. Even if copulation had been observed, the time relationship between copulation and ovulation is not known. The only guide in estimating the age of the corpus luteum is the age of the embryo within the oviducts. •

When the egg is still without shell membranes and segmentation has only just begun, the follicle has already begun to recover from its collapse (Plate ix, fig. 1). The torn fibrous connective tissue beneath the follicular epithelium is repaired; the capillaries are now numerous and are interspersed among irregular

nests of theca interna cells, which are in a state of active growth. The cells of the follicular epithelium have begun to divide, filling the interstices between the folds. They divide mitotically and amitotically, but mitotic figures are rare.

The corpus luteum at the stage when the medullary folds have begun to develop.—At this stage the eggs are still without shell. There is no change in the size of the follicle. The follicular epithelial cells have filled the clefts between the folds and there is only a suggestion of the original form of the folds. The walls of the follicle may converge (Plate ix, fig. 2); the cicatrix is still evident and there may be blood clots and cell débris within the cavity of the follicle. The epithelial cells have the same structure as at earlier stages, although in some specimens the cells nearest the theca interna may have particularly deeply staining nuclei (Plate x, fig. 1). Connective tissue fibres and a few spindle-shaped fibroblastic cells have grown up from the theca interna into the folds of the follicular epithelium, capillaries are developing.

The corpus luteum when the unflexed embryo lies on its side on the yolk-sac and the allantois is a small swelling at the posterior end of the embryo.—The corpus luteum is now kidney-shaped and is filled with follicular epithelial cells which will henceforth be termed "luteal cells" (Plate ix, fig. 3; Pl. x, fig. 2). The form of the original folds may still be recognized at the periphery of the luteal tissue. The luteal cells have irregular shapes and in some specimens the cell walls are more distinct than in others. Also in some specimens all the nuclei take a deep stain, while in others some may stain deeply and some lightly. The spindle-shaped fibroblastic cells have penetrated throughout the luteal tissue and there may be a thick core of such fibrous tissue at the centre of the corpus luteum carrying comparatively large blood vessels. These fibroblastic cells are definitely associated with the blood vessels and do not ramify among the individual luteal cells. The connective tissue fibres alone penetrate between the luteal cells. There is less sheath tissue than at earlier stages (Plate x, fig. 2).

The corpus luteum immediately before egg laying.—At this stage the embryo is flexed, the heart visible as a swelling at the anterior end, and the allantois enlarged to about 3 mm. in diameter. This is the oldest stage found in the eggs within the oviducts and is apparently the most advanced stage reached by the embryo at the time of the laying of the eggs. From a comparison with the embryos of the viviparous *L. (Hinulia) quoyi*, it is possible to estimate approximately that the embryo of *A. muricatus* is about ten days old at this stage (see description of *L. (Hinulia) quoyi* below).

The corpus luteum is shrunken and measures approximately 1.2 mm. \times 0.5 mm. (Plate ix, fig. 4), and the luteal cells have all the appearances of degeneration (Plate x, fig. 3). The cell cytoplasm is more vacuolated than at earlier stages and easily splits during fixation and embedding. The nuclei are shrunken and collapsed and even pycnotic. The degenerating tissue is deeply impregnated by septa of fibroblastic cells of the theca interna. Few of the sheath tissue cells are degenerating.

The fate of the corpus luteum after the laying of the eggs.—At the time of the first ovulation the ovary contains, as well as the large ova ready for ovulation, a number of small ova with a diameter of approximately 1 or 2 mm. After ovulation, and while the lizard carries eggs within the oviducts and corpora lutea within the ovaries, these small ova begin to enlarge, obviously, as described above, in preparation for a further breeding season, and by the time of the

laying of the eggs these developing ova may measure as much as 6 mm. in diameter (Plate ix, fig. 4). When the ova have attained a diameter of about 10 mm. the eggs have been laid and all the corpora lutea have disappeared from the ovaries. In one lizard, which laid its eggs on 29th November, the corpora lutea had all disappeared by the 11th December. If the period of non-pregnancy between the breeding seasons is approximately two weeks, as supposed, the "post-partum" existence of the corpus luteum within the ovary must be something less than two weeks.

The corpora lutea of the different breeding seasons are naturally identical in structure, but those of the first pregnancy are associated with developing ova and those of the last pregnancy with atretic follicles. During the last pregnancy even medium-sized ova are atretic, and after the laying of the eggs the corpora lutea degenerate among degenerating follicles.

The corpus luteum in the viviparous lizard Lygosoma (Hinulia) quoyi.

In *L. (Hinulia) quoyi* there is no apparent reduction in the yolk-content of the ovum at the time of ovulation and there is only a simple allanto-placenta, presumably for respiration.

Specimens of *L. (Hinulia) quoyi* were collected from the heights of Elanora, in the environs of Sydney, during October, 1932. Until the 20th October no pregnant lizards were found, although, judging from their size, the ova in the ovaries were almost ready for ovulation. On the 24th October eight of the ten females collected were pregnant, so that it was possible to determine within a few days the time of ovulation and the age of the developing embryos. Such regularity among viviparous lizards is by no means the rule, as is shown by a comparison of the dates of various stages in the development of the embryos of specimens of *L. (Hinulia) quoyi* collected from other localities.

The ovary at the time of ovulation is essentially similar in structure to that of the oviparous *A. muricatus* described above, so that further description is unnecessary here. The mature ova are also approximately the same size as those in *A. muricatus*, measuring about 10 mm. in diameter.

The corpus luteum in early stages of development.—The youngest corpus luteum examined was taken from a lizard collected on the 25th September, 1933. There were no signs of egg segmentation or of shell membrane. The burst follicles were flaccid and bloody and had collapsed down to about 2.5 mm. \times 1 mm. The follicular epithelium is a deeply folded single layer of cuboid cells with deeply-staining cytoplasm and round, lightly-staining, vesicular nuclei. The sheath tissue resembles that described above for *A. muricatus* at a similar stage.

The next earliest stage in the development of the corpus luteum was collected on the 25th September, 1933. The embryonic shield was visible in the eggs and the burst follicles were tauter and less bloody, although well vascularized by vessels in the sheath tissue visible to the naked eye. In section the original folds of the follicular epithelium are still evident as a columnar arrangement of the epithelial cells upon the underlying theca interna. The interstices of the folds have been filled with epithelial cells. At this stage there is often the same variation in staining as occurs among the nuclei of the follicular epithelial cells of *A. muricatus*, some of the nuclei taking a light stain in iron haematoxylin and others a deep stain.

The corpus luteum when the embryo lies on its side on the yolk-sac and the allantois is a small diverticulum.—Lizards with embryos at this stage in develop-

ment were collected on the 9th and 15th October, 1933. The corpus luteum is now solid, but is still a flat sac and measures approximately 2 mm. \times 1 mm. (Plate x, fig. 4). As in *A. muricatus*, the corpus luteum has been mostly filled by the amitotic division of the follicular epithelial cells. The luteal cells at this stage are comparatively long and narrow, often with indefinite cell limits, and the nuclei may take either a light or dark stain from iron haematoxylin (Plate xii, fig. 2). The sheath tissue is unchanged. The theca interna fibroblasts do not grow among the luteal cells. The corpuscles are concentrated in the theca interna immediately beneath the luteal cells (Plate x, fig. 4).

The corpus luteum at about the middle of the second week of pregnancy, when the limbs are developing and the allantois has united with the chorion.—The females with embryos at this stage in development were collected on 15th and 22nd October and on 9th November, 1933. The corpus luteum is now kidney-shaped with dimensions about 1.5 mm. \times 1 mm. (Plate xi, fig. 1), and is densely packed with luteal cells of irregular shape, with or without distinct cell limits. The luteal cells are only approximately half the size of those at earlier stages, although the nuclei are apparently unchanged (compare the luteal cells in Plate xi, figure 3, with those in Plate xii, figure 2). The cicatrix is healed by fibrous tissue from the sheath and is plugged with luteal cells. The sheath is thinner than at earlier stages, due to a superficial penetration between the luteal cells by the spindle-shaped fibroblastic cells of the theca interna (Plate x, fig. 1). However, the penetration does not extend far and there are never any blood vessels within the corpus luteum among the luteal cells.

The corpus luteum at the stage when the digits of the embryo are differentiating and the chorio-allantoic vesicle fills about one-third of the incubatory chamber.—Lizards with young at this stage of development were collected on 10th, 15th, and 22nd November, 1933. The corpus luteum may be spherical or kidney-shaped, and still measures approximately 1.5 mm. \times 1 mm. The luteal cells have the same appearance as at the stage described above. The sheath tissue is now reduced to about one-half its original width, and at the periphery the luteal cells are cut into numerous "nests" by the theca interna.

From this stage on, until the embryo is well advanced in development, has acquired pigmented scales and is approximately at the end of the second month of the gestation period, there is no obvious change in the structure of the corpus luteum, but at about the end of the second month the first signs of degeneration of the luteal cells appear. The luteal cells at the centre of the corpus luteum become enlarged and vacuolated and their nuclei are collapsed and shrunken (Plate xi, fig. 2). Also a peculiar, dense, pink-staining coagulum often appears amongst the luteal cells and at the periphery of the corpus luteum between the luteal cells and the theca interna. There are only a few isolated degenerating cells in the sheath tissue. The degeneration of the luteal cells once begun continues until, by the time the embryo has reached a stage in development where the yolk-sac is withdrawn into the alimentary canal and the time of birth is obviously near, the degeneration has spread throughout the luteal cells (Plate xi, fig. 4). Degeneration is assumed from the vacuolated appearance of the cell cytoplasm, the breaking down of the nuclear membrane and the general collapse and shrinkage of all the nuclei. The progress in degeneration is accompanied by an increase in the amount of coagulum between the luteal cells. Since the coagulum increases as the degeneration progresses, it is thought to be probably a product of that degeneration.

The corpus luteum at the time of birth.—Pregnant females of *L. (Hinulia) quoyi* were kept in captivity during the last few weeks of their pregnancy so that the birth of the young could be observed and corpora lutea obtained from the females while giving birth to young. The ovaries were taken from five lizards in this condition (Plate xii, fig. 3). The luteal cells show widespread degeneration (Plate xii, figs. 4, 5), and in one specimen of *L. (L.) weekesae* examined at a similar stage, the corpus luteum was so filled with coagulum, that it was at first mistaken for a gland in the process of active secretion (Plate xiii, fig. 5). However, the great decrease in the number of luteal cells, and the dead or dying state of those present, strongly suggest that the coagulum is no more than a product of the degeneration of the luteal cells.

Those lizards observed gave birth to young at intervals ranging from ten minutes to two hours between each birth, and the members of each litter, with the exception of those from one particular female, were all born within twenty-four hours of the first birth. From this particular female two young were born on 13th February, 1933, and a third nine days later, on 22nd February.* It would be interesting to observe other lizards to see if this irregularity is a common habit, for if the habit is a common one these lizards would be the only amniota known to give birth to young of the same litter at such widely separated intervals. And it would be interesting to investigate the fate of the corpora lutea under such conditions. Is the birth of each foetus accompanied by the disappearance of one corpus luteum, do the corpora lutea all disappear after the first birth, or do they all persist until the last birth? The ovaries of the female mentioned above were examined twenty-four hours after the birth of the last foetus and all three corpora lutea were in the last stages of degeneration.

The degeneration of the corpus luteum after the birth of the young.—The type of luteal degeneration after the birth of the young is typical for all the lizards examined, and at first sight the degenerating corpus luteum may be mistaken for a degenerating follicle. The luteal cells enlarge enormously, and are greatly vacuolated (Plate xii, fig. 6). The coagulum between the luteal cells and the theca interna is thrown into folds as the corpus luteum shrinks. In their degeneration the sheath tissue cells are also enlarged and vacuolated. The corpus luteum is last visible as a small orange speck among the ova. There were no corpora lutea in the ovaries of females examined two weeks after the birth of the young.

The corpus luteum in the Australian viviparous lizards *Egernia whitei*, *Lygosoma (Hemiergis) quadridigitatum*, *E. cunninghami*, *Lygosoma (Liolepisma) weekesae*, *L. (L.) entrecasteauxi* and the European lizard *Lacerta vivipara*.

E. whitei and *L. (Hemiergis) quadridigitatum* are both lizards with no apparent reduction in the yolk-content of the ovum at the time of ovulation and with a simple allanto-placenta presumably for respiration. The corpus luteum has fundamentally the same structure in both lizards, and is essentially similar to that described above for *L. (Hinulia) quoyi*. There are the same small, round luteal cells with round, or sometimes oval, lightly-staining nuclei; there are only

* These dates are much later than those given for the birth of the young among specimens of *L. (Hinulia) quoyi* collected around Sydney. The lizard referred to was caught at Jenolan, which has a much later spring than Sydney.

superficial ingrowths of fibroblasts among the luteal cells and consequently there are no blood vessels among the luteal cells (Plate xiii, fig. 1).

E. cunninghami is the largest lizard examined, and the sac-like corpus luteum measures as much as 5 mm. \times 3 mm. The sheath tissue is correspondingly thick and has the same structure as that described for *A. muricatus* and *L. (Hinulia) quoyi*. The luteal cells are also essentially similar to those described for the other lizards, except that they also include scattered giant cells (Plate xiii, fig. 2). There are large blood vessels and blood clots among the luteal cells, but since these have very little supporting tissue from the theca interna and often no distinct vessel walls, they are thought to be in traumatic cavities formed by the tearing of the follicle wall on the expulsion of the large egg. There are none of the ingrowing septa of fibroblasts from the theca interna so characteristic of *A. muricatus*.

L. (L.) weekesae and *L. (L.) entrecasteauxi* are two closely related skinks and are both restricted to high altitudes. With *Chalcides tridactylus* in Italy, these lizards have the most highly specialized allanto-placenta so far found among reptiles. As in all other viviparous lizards examined, the corpus luteum is present within the ovary until a few weeks after the birth of the young, that is, for approximately three and a half months. The mature corpus luteum in each species is spherical, measures about 0.5 mm. in diameter, and is the smallest corpus luteum yet found among lizards (Plate xiii, fig. 3). The sheath tissue is correspondingly thin, but the theca externa and interna are well differentiated. The theca interna contains spindle-shaped fibroblastic cells whose nuclei may be twice the size of those of the luteal cells (Plate xii, fig. 4). The fibroblastic cells penetrate the luteal tissue providing blood vessels and dividing the luteal tissue into nests of cells. As in *A. muricatus*, the fibroblastic cells are definitely associated with the blood vessels and do not ramify between the individual luteal cells. Only the connective tissue fibres penetrate between the cells.

As in *L. (Hinulia) quoyi* the luteal cells begin to degenerate within a month of the birth of the young, and by the time of birth all the luteal cells are dead or dying. As mentioned above, in one of the specimens of *L. (L.) weekesae*, examined while the young were being born, many of the luteal cells had disappeared and the "nests" were filled with coagulum, the whole corpus luteum having something of the appearance of a mammary gland (Plate xiii, fig. 5). The corpora lutea in both ovaries had the same structure, and when they were first examined it was thought that the tissue may be glandular and in the act of secreting the coagulum. And, curiously enough, a coagulum of similar appearance occurred in globules at the surface of the uterine wall surrounding the embryos (Plate xiv, fig. 1). But a closer examination showed that the luteal cells were either dead or dying and the coagulum was thought to be merely a product of the cell degeneration.

Lacerta vivipara is a small viviparous skink. Specimens were collected from the Auvergnès mountains during July, 1931, and from the Pyrenees and the French Alps in August, 1931. The available material consists of two females with young corpora lutea, eleven with old degenerating corpora lutea, twenty with corpora lutea of "post-partum", and the ovaries of five females were examined while the young were being born.

Like *L. (L.) weekesae* and *L. (L.) entrecasteauxi*, *Lacerta vivipara* has a corpus luteum that measures only 0.5 mm. in diameter. The sheath tissue has

the same structure as that described above for the Australian lizards, and is well illustrated by figure 2 on Plate xiv. At the youngest stage examined, the corpus luteum is a flat sac, filled with luteal cells, which have not yet been invaded by the sheath tissue (Plate xiv, fig. 2). The luteal cells are bigger than those in the corpus luteum of any Australian lizard so far examined, and most closely resemble the mammalian luteal cells.

Unfortunately the only other stages available are old, within a few weeks, and even days, of birth. At this stage the luteal tissue is degenerating. The luteal cells are slightly larger than at earlier stages, and the cell cytoplasm is vacuolated and many of the cell nuclei are shrunken. The degeneration first begins at the centre of the corpus luteum. In figure 3 on Plate xiv, some of the luteal cells at the periphery still have the appearances of healthy cells. A coagulum, similar to that described above for other lizards, occurs among the luteal cells at the time of the birth of the young. The luteal tissue now contains the spindle-shaped fibroblastic cells of the theca interna, which are not only associated with the blood vessels, but penetrate between the luteal cells (Plate xiv, fig. 3). The sheath tissue is greatly depleted (Plate xiv, fig. 4), and may consist of no more than one or two layers of connective-tissue cells.

DISCUSSION.

After much discussion about the types of luteal cells in the mammalian corpus luteum, the function of the cells of the theca interna within the corpus luteum and the nature and function of the ovarian interstitial tissue, the general consensus of opinion at the moment seems to be that the luteal cells are formed by the hypertrophy of the follicular epithelium (Hill and Gatenby, 1926), that the fate of the theca interna is still a matter of dispute, the problem being complicated by histological species differences (Deanesly, 1930b), and that the whole problem of determining the part played by the interstitial tissue "is complicated by the lack of any agreed definition of interstitial tissue and by the uncertain behaviour of atretic follicles" (Parkes, 1929). In reptiles the luteal cells are without doubt derived from the follicular epithelial cells, and there are also differences in the behaviour of the theca interna cells in different genera of lizards, but these differences do more to illuminate than to complicate an understanding of the significance of the theca interna. Among the one reptilian family Scincidae there are at least three different types of behaviour of the theca interna, and yet the type of reproductive cycle in each species is fundamentally similar: (1) In the viviparous skinks *L. (Hinulia) quoyi*, *L. (Hemiergis) quadridigitatum* and *E. whitei*, there are no ingrowths of theca interna fibroblasts among the luteal cells; (2) In the viviparous skinks *L. (L.) weekesae* and *L. (L.) entrecasteauxi* the fibroblasts grow amongst the luteal cells in definite strands, providing the luteal cells with blood vessels. These fibroblasts are only associated with the blood vessels and do not penetrate between the individual luteal cells; (3) In the viviparous skink *L. vivipara* there are the same septa of theca interna cells providing the blood vessels and in addition the fibroblastic cells do penetrate between the luteal cells. There are no variations in the particular reproductive cycle of any of these lizards to account for these differences. Certainly *L. (L.) weekesae* and *L. (L.) entrecasteauxi* have a comparatively highly specialized allantoaplacenta, but ingrowths of fibroblasts among luteal cells cannot be particularly associated with placentation as it occurs in the oviparous lizards *A. muricatus* (as described

above) and *L. agilis* (Hett, 1924). Nor can the differences in corpus luteum vascularization and theca interna invasion be associated with a variation in the size of the ripe follicles, as is suggested for the mammals (Deanesly, 1930b).

Marshall (1922), after mentioning Mingazzini's belief that the corpus luteum in reptiles "is identical with the mammalian corpus luteum", wrote "it is noteworthy that the above mentioned animals (reptiles) which show luteal hypertrophy are all viviparous". But further investigations (Hett, 1924, and the present investigation) have shown that luteal formation is to be also associated with oviparity.

The corpus luteum in the oviparous lizard *A. muricatus* disappears soon after the laying of the eggs, having had an intra-ovarian existence of approximately three weeks. The corpus luteum in the viviparous lizards remains in the ovary throughout the gestation period of three months and disappears within two weeks after the birth of the young. There is, then, perhaps some relationship between the presence of the corpus luteum within the ovary and the retention of the eggs within the oviduct.

In the viviparous lizards atresia of ova begins early in the gestation period and continues until the birth of the young. It seems more likely that such atresia is controlled by some factor other than the presence of corpora lutea within the ovary, as had been suggested for mammals, since in the oviparous *A. muricatus* ova develop to within a short time of ovulation in the presence of healthy corpora lutea.

SUMMARY.

A description is given of the development and structure of the corpus luteum in oviparous and viviparous lizards. In all the lizards examined the luteal cells are formed by the division, mitotic and amitotic, of the cells of the follicular epithelium. Mitotic figures are rare. The behaviour of the theca interna varies with the subgenus of the lizard. In the oviparous lizard *Amphibolurus muricatus* the spindle-shaped fibroblastic cells of the theca interna grow among the luteal cells, providing blood vessels. These fibroblasts are definitely associated with the blood vessels, and only connective tissue fibres extend between the individual luteal cells. In the viviparous lizards *Lygosoma (Hinulia) quoyi*, *L. (Hemiergis) quadridigitatum*, *Egernia whitei* and probably *E. cunninghami*, there are no ingrowths of thecal fibroblasts among the luteal cells. In the viviparous lizards *L. (Liolepisma) weekesae* and *L. (L.) entrecasteauxi*, two lizards with a comparatively highly specialized allanto-placenta, there are definite ingrowths of theca interna fibroblasts, but, as in *A. muricatus*, only connective tissue fibres actually penetrate between the individual luteal cells. In the viviparous *Lacerta vivipara* and, according to Hett, the oviparous *Lacerta agilis*, not only are the fibroblastic cells of the theca interna associated with blood vessels among the luteal cells, but they also penetrate between the individual luteal cells.

In the oviparous *A. muricatus* the corpus luteum has an intra-ovarian existence of approximately three weeks, degeneration of the luteal tissue beginning while the lizard is still carrying the eggs and continuing until the time of egg laying, when all the luteal cells are either dead or dying.

In the viviparous lizards the corpus luteum has an intra-ovarian existence of approximately three and a half months, degeneration beginning at about the end of the second month of pregnancy and continuing during the last month of

pregnancy until, by the time of the birth of the young, the degeneration has spread throughout the luteal tissue.

The oviparous *A. muricatus* has at least two breeding seasons each summer. The viviparous lizards have but one annual breeding season. In the viviparous species atresia begins during the early stages of pregnancy while the ova are quite small. In the oviparous lizard atresia rarely occurs during the first pregnancy; ova enlarge in preparation for a second breeding season in the presence of healthy corpora lutea in the ovary and also in the presence of eggs within the oviducts.

DESCRIPTION OF PLATES IX-XIV.

Abbreviations.—*b.v.*, blood vessel; *c.*, coagulum; *d.l.*, degenerating luteal cells; *f.b.*, fibroblastic cell of theca interna; *f.c.t.*, connective tissue fibres; *f.e.*, follicular epithelial cells; *t.e.*, theca externa; *t.i.*, theca interna; *s.t.*, degenerating sheath tissue.

Plate ix.

Fig. 1.—Follicle of *A. muricatus* after expulsion of the ovum, showing the sheath tissue and folded follicular epithelium. $\times 20$.

Fig. 2.—Follicle of *A. muricatus* at the stage when the medullary folds have begun to develop in the eggs within the oviducts. $\times 20$.

Fig. 3.—Mature corpus luteum of *A. muricatus* showing ingrowths of fibroblasts among the luteal cells. $\times 60$.

Fig. 4.—Corpus luteum of *A. muricatus* at the time of laying of the eggs in the company of several enlarged ova which are preparing for a further breeding season. $\times 20$.

Fig. 5.—Section through the folded follicular epithelium of *A. muricatus* at the stage illustrated by figure 1, showing the tear between the theca interna and the epithelial tissue and a few loose cells and capillaries. $\times 375$.

Plate x.

Fig. 1.—Section through the edge of the corpus luteum of *A. muricatus* at the stage illustrated by figure 2 on Plate ix, showing ingrowths of spindle-shaped fibroblastic cells from the theca interna. $\times 375$.

Fig. 2.—Section through the mature corpus luteum of *A. muricatus*. $\times 375$.

Fig. 3.—Section through the degenerating corpus luteum of *A. muricatus* at the stage immediately prior to egg laying. $\times 375$.

Fig. 4.—Young corpus luteum of *L. (Hinulia) quoyi* showing cicatrix, luteal cells, theca externa and interna. $\times 40$.

Fig. 5.—Ovary of *L. (Hinulia) quoyi* showing relationship in size between a young corpus luteum and the remainder of the ovary. $\times 20$.

Plate xi.

Fig. 1.—Corpus luteum of *L. (Hinulia) quoyi* at the middle of the second week of pregnancy showing superficial ingrowths of theca interna among the luteal cells. $\times 60$.

Fig. 2.—Corpus luteum of *L. (Hinulia) quoyi* at the end of the second month of pregnancy showing the first signs of the degeneration of the luteal cells. $\times 50$.

Fig. 3.—Section through the edge of a corpus luteum of *L. (Hinulia) quoyi* at the stage illustrated by figure 1 on Plate xi, showing the reduction in size of the luteal cells since the stage illustrated by figure 2 on Plate xii, and the darkly and lightly staining follicular epithelial cells. $\times 375$.

Fig. 4.—Section through the edge of a degenerating corpus luteum of *L. (Hinulia) quoyi* immediately before the birth of the young. $\times 375$.

Plate xii.

Fig. 1.—Section showing superficial ingrowth of the theca interna of *L. (Hinulia) quoyi* among the luteal cells and the "nests" of cells so formed. $\times 375$.

Fig. 2.—Section through the edge of a young corpus luteum of *L. (Hinulia) quoyi* showing lightly and darkly staining follicular epithelial cells. $\times 375$.

Fig. 3.—Ovary of *L. (Hinulia) quoyi* showing the relationship between the corpus luteum and the rest of the ovary at the time of the birth of the young. $\times 19$.

Fig. 4.—Section through the edge of a degenerating corpus luteum removed from a lizard giving birth to young, showing the coagulum and degenerating luteal cells. $\times 375$.

Fig. 5.—Section through the entire corpus luteum removed from a lizard giving birth to young. $\times 47$.

Fig. 6.—Section through the degenerating corpus luteum of *L. (Hinulia) quoyi* after the birth of the young. $\times 60$.

Plate xiii.

Fig. 1.—Section through the edge of a corpus luteum of *E. whitei* at the end of the second week of pregnancy when the corpus luteum is considered mature. $\times 375$.

Fig. 2.—Section through edge of a mature corpus luteum of *E. cunninghami* showing a few scattered giant cells. $\times 375$.

Fig. 3.—Corpus luteum of *L. (L.) weekesae* at the end of the first month of pregnancy. $\times 120$.

Fig. 4.—Section of the interior of the corpus luteum of *L. (L.) weekesae* at the stage when there is little yolk left within the yolk-sac of the developing embryos and the embryos are in an advanced stage of development, showing the degeneration of the luteal cells and the large healthy nuclei of the spindle-shaped cells of the theca interna. $\times 375$.

Fig. 5.—Section through the edge of the corpus luteum of *L. (L.) weekesae* taken from a lizard while giving birth to young, showing the degeneration of the luteal tissue and the presence of coagulum within the corpus luteum. $\times 375$.

Plate xiv.

Fig. 1.—Section through one of the folds in the uterine wall in the placental area of *L. (L.) weekesae* showing the globules of coagulum. $\times 375$.

Fig. 2.—Part of a young corpus luteum of *L. vivipara* showing the theca externa, theca interna and the large luteal cells. $\times 80$.

Fig. 3.—Section through the edge of a corpus luteum of *L. vivipara* immediately before the birth of the young, showing the blood vessels among the luteal cells and the spindle-shaped cells of the theca interna between the luteal cells. $\times 375$.

Fig. 4.—The corpus luteum of *L. vivipara* immediately before the birth of the young, showing the much depleted sheath tissue and its ramification among the luteal cells. $\times 80$.

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